

GONDWANALAND CONNECTIONS IN THE TERRESTRIAL MOLLUSCS OF AFRICA AND AUSTRALIA¹

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SUMMARY

Africa and Australia share only two Gondwanaland families, the Rhytididae and Charopidae. In a bicontinental pattern the former are rather diverse in the Australian Region and only sparsely represented in Africa; the latter are of somewhat comparable diversity in both continents, but appear to be very diverse elsewhere (e.g., New Zealand), while exhibiting a tri continental pattern. The evolutionary success of these and other Gondwanaland families has been markedly poor in Africa as compared to that in the other remnants of Gondwanaland. This may be explained by the island history of Africa and its subsequent contact with Eurasia (Laurasia); once this was established the vigorous and diverse Eurasian elements started invading Africa from the north replacing the Gondwanaland —elements or frustrating their northward dispersal. Both Australia and South America remained comparatively much more isolated, so that the Gondwanaland elements retained or established a comparatively much more dominant position.

Biogeography in general has recently received new impulses mainly as regards its theoretical background such as the new phylogeny and the stunning geological contributions known as the complex of continental drift, plate tectonics and palaeomagnetism. Biogeography of land molluscs is still in its infancy because of factors such as the large number of species involved, poor knowledge of their relationships consequent on limited anatomical data and as yet poorly understood distribution patterns. The biogeography of terrestrial gastropods has virtually entered a new era since Solem's paper (1959) on the New Hebrides.

Africa south of the Sahara harbours a rich fauna of land snails, recently estimated at ca. 6000 species (Van Bruggen, 1977). The species of the southern parts of the continent are of particular interest since their distribution essentially reflects a bipolar pattern, namely elements of northern origin intimately intermixed with elements of southern origin (Van Bruggen, 1969). Most of the southern elements may be termed Gondwanaland elements. Gondwanaland families are here defined as families that mainly show a distribution on one or more fragments of ancient Gondwanaland.

Some southern distribution patterns in Africa do not have a Gondwanaland origin but represent relict elements of families with northern (Laurasian) distribution patterns. In southern Africa the Oopeltinae (a group of endemic slugs) are a subfamily of the Holarctic

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Arionidae and the genus *Fauxulus* (— perhaps also *Afriboysidia*) belongs to the Palaearctic family Orculidae. These are palaeogenic elements irrelevant to the topics discussed here (vide Van Bruggen, 1969: 101, 1978: 896).

The terrestrial molluscs of the Ethiopian or Afrotropical and Australian Regions have comparatively little in common. Apart from a limited number of cosmopolitan or near-cosmopolitan families and some circumtropical or near-circumtropical groups, there are two Gondwanaland families. The first category, the near-cosmopolitan families, consists of groups such as the Pupillidae *sensu lato*, the Valloniidae and Succineidae, the latter two only sparsely represented in both regions. The second category, the near-circumtropical families, encompasses groups such as the Subulinidae (sparsely represented in Australia, but very diverse in Africa and elsewhere). The two Gondwanaland families are the Rhytididae or Paryphantidae, and the Charopidae (Sølem, 1976, 1978), formerly part of the large complex called Endodontidae (see, e.g., Zilch, 1959) and in that context cosmopolitan.

As regards Gondwanaland — families, the Ethiopian Region harbours five families of terrestrial pulmonates that may be regarded as belonging to this category, the Aperidae, Dorcasiidae, Corillidae, Charopidae, and Rhytididae (Van Bruggen, 1977, 1978). All occur in southern Africa in a wider sense; table 1 shows their status in Africa, their possible relationships in the form of surmised sister groups and the distribution of these. The Aperidae are small to fairly large (ca. 25-120mm when alive) carnivorous slugs; the sister group may be the family Rhytididae. Incidentally, the range of the Aperidae more or less coincides with that of the African Rhytididae (Van Bruggen, 1978, figs. 8 and 7a). The

family	status in Africa (all southern Africa s.l.)	sister groups and its distribution
Aperidae	endemic family, 1 genus (<i>Apera</i>) with 12 species	? Rhytididae: South Africa, Seychelles, New Guinea and as far west as Borneo, Australia, New Caledonia, New Zealand, SW Pacific Islands
Dorcasiidae	endemic family, 3 genera with 1 species (<i>Tulbaghinia</i>), 4 species (<i>Dorcasia</i>), and 10 species (<i>Trigonephrus</i>) respectively	Strophocheilidae (+ Megalobulimidae): South America
Corillidae	1 endemic genus (<i>Sculptaria</i>) with 16 species	Corillidae of southern Asia
Charopidae	probably ca. 20 endemic genera with ca. 120 species	other Charopidae elsewhere
Rhytididae	2 endemic genera with 5 species Rhytididae (<i>Nata</i>) and 17 species (<i>Natalina</i>) respectively	Australian + New Zealand

TABLE 1. African (i.e., Ethiopian Region) pulmonate Gondwanaland families.

Dorcasiidae, another endemic family with a slightly more diverse pattern (Van Bruggen, 1977, fig. 1; 1978, fig. 6), have fairly large to large shells (8.0-39.5 x 15.0-45.0mm) and are desert and semidesert snails (with one exception in the mountains of the south western Cape Province). The giants of South America, the Strophocheilidae with the recently separated Megalobulimidae (Leme, 1973), are most likely to be the vicariant sister group of the Dorcasiidae (cf. Solem, 1978:91). The Corillidae in Africa consist of a single genus, *Sculptaria*, with a fair diversity as regards species, which are all small (major diameter of

shell 5-10mm) desert and semidesert dwellers (Van Bruggen, 1978, fig. 4). The sister group of these most probably is the remaining part of the family which shows a more or less continuous vicariant distribution in southern Asia. Among the African Gondwanaland pulmonates the Charopidae show the greatest diversity. The taxonomy of the ca. 120 known species (Connolly, 1939; Van Bruggen & Verdcourt, 1965; Solem, 1970; Sirgel, 1980), all smallish to very small indeed (major diameter of shell 1.2-23.3mm), has not been sufficiently worked out, except for one genus endemic to southern Africa, *Afrodonta*, with eleven species (Solem, 1970). At the moment almost all other species are classified with the genus *Trachycystis*, of which ca. twenty subgenera and subgeneric units are distinguished. Subgeneric units are as yet unnamed taxa probably of subgeneric rank. It is quite likely that these may be raised to generic rank when properly revised. In the mollusc fauna of southern Africa the Charopidae form a dominant element (Van Bruggen, 1978, fig. 1, for

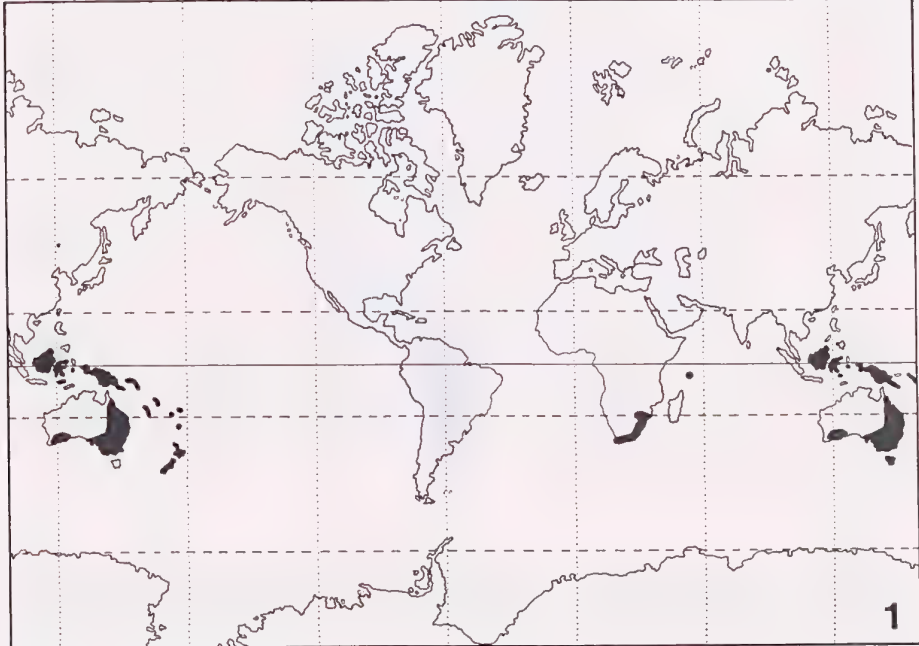


FIGURE 1. World distribution of the pulmonate family Rhytididae (Paryphantidae); note isolated occurrence on Seychelles Islands north of Madagascar.

RHYTIDIDAE (= Paryphantidae)

data after Connolly, 1939 (southern Africa, with corrections)

Burch, 1976 (Australia)

Powell, 1976 (New Zealand)

area	total Pulmonata species genera		Rhytididae genera % of total		Rhytididae species % of total	
Southern Africa	635	69	2	3%	22	3%
Australia	707	188	13	7%	42	6%
New Zealand	294	44	5	11%	35	12%

(some data approximate)

TABLE 2. Local diversity of the pulmonate family Rhytididae (Paryphantidae) in Africa, Australia and New Zealand.

Endodontidae substitute Charopidae, because in Solem's new taxonomy almost all species will be classified with that family except for a few Punctidae). Dominant families, loosely defined, are families that by virtue of their local diversity make up a significant segment of the total number of species, e.g., Camaenidae in Australia and Helicidae around the Mediterranean. It is well-nigh impossible to guess what the sister group of the African Charopidae is; the family as a whole is very widely distributed in the southern hemisphere and at the same time shows a remarkable diversity in the Australian Region *sensu lato*.

Finally, the Rhytididae are in Africa represented by two endemic genera with a total of 22 species (Van Bruggen, 1978), carnivores varying in size from very small to very large (major diameter of shell 4.5-75.5mm). The two southern African genera form a compact group; possibly the Australian and New Zealand Rhytididae together form the vicariant sister group of the African Rhytididae, which leaves the problem of the few taxa on the western Indian Ocean island group of the Seychelles (genus *Priodiscus*). The African distribution of the family (Van Bruggen, 1978, fig. 7a) shows that the two genera only occupy the humid southeastern parts of the continent on and east of the escarpment. The world distribution of the family (fig. 1; see also Solem, 1979, fig. 4) shows a typical Gondwanaland pattern, although the group is not represented in either Madagascar or South America (bicontinental pattern). The Rhytididae have penetrated far northwest, as far as Borneo, thus beyond Wallace's line. At present the greatest diversity of the family is in the Australian Region (table 2). This table features the comparative role of the Rhytididae on the main land areas Africa, Australia and New Zealand. Attention should be drawn to the increasing importance of the family from west to east. In southern Africa the Rhytididae are a numerically comparatively very insignificant group with only 3% of the genera and of the species. In Australia the family is roughly twice as important, whatever these figures stand for. However, in New Zealand the Rhytididae are a dominant family with 11% of the genera and ca. 12% of all pulmonate species, or double the figures for Australia which implies four times those for Africa. Outside these large land areas the Rhytididae are found on a host of larger and smaller islands, although to my knowledge never in such a dominant position. In New Guinea, for example, there are only two non-endemic genera and a total of only six species (Van Benthem Jutting, 1964). This is perhaps a naturally impoverished number of taxa, a low diversity near the northernmost limits of the distribution.

Rhytididae are powerful carnivores, feeding on what is somewhat indifferently called 'soft invertebrates', mainly other snails "such as achatinids and subulinids and possibly any other snail sufficiently common to fall victim to these predators' (Van Bruggen & Appelton, 1977: 33). In Africa various groups of snails seemingly compete for the same niches, viz., carnivorous slugs of the family Aperidae (largely sympatric with the Rhytididae), and the very diverse, almost circumtropical family of the Streptaxidae. Members of the latter family are generally small to very small (shell length 1.5-21.5mm) where they are sympatric with the Rhytididae, although species of about equal size are known to occur together. The real giants among the streptaxids (*Edentulina*, shell up to ca. 50mm long) occur in Central Africa and in Madagascar where there are no Rhytididae. No information is available as regards carnivorous snails seemingly competing with the Rhytididae outside Africa, except for the Seychelles Islands where the few small and insignificant rhytidids are sympatric with a fairly diverse assemblage of streptaxids (Mahe: 1 *Priodiscus* and 13 Streptaxidae; Praslin: 1 *Priodiscus* and 3 Streptaxidae; Silhouette: 2 *Priodiscus* and 7 Streptaxidae; data from Sykes, 1909).

The second Gondwanaland pulmonate family shared by Africa and Australia is the Charopidae. The state of the taxonomy of the family in Africa does not allow one to extensively dwell upon this group. Fig. 2 shows the world distribution of the family with data from outside Africa mainly derived from a number of papers by Solem and additional information supplied by this author (in litt., 1979); although almost completely limited to the southern hemisphere the range appears to be considerable. The distribution in Africa covers a limited area in southeastern Africa with headquarters in Natal, while petering out quickly north of the Zambezi River with a few species reaching the equator in Kenya. As

yet there are no exact figures available for comparing the known diversity in Africa with that elsewhere; the few data are set out in table 3. All numerical data exclude newly discovered but as yet unpublished species. According to Dr. Solem (in litt., 1979) Burch (1976 : 132-133 s.n. Punctidae) enumerates 30 genera with a total of 109 species considered Charopidae by the former, viz. Burch's Endodontinae (pp. 132-133 minus *Theskelomensor*) and Phenacohelicinae (p. 133). The data for Africa and Australia show generic diversity in the Charopidae in Australia yet to be less than in Africa, while data on the species level do not seem to differ significantly. The position in New Zealand, the southwest Pacific islands and elsewhere is utterly different. According to Dr. Solem (in litt., 1979) Powell (1976: 115-119) enumerates 19 genera with a total of 145 species considered Charopidae by the former, viz. Powell's Endodontidae (pp. 115-116), Flammulininae (pp. 116-118) and Otoconchinae (p. 119). The malacofauna of New Zealand shows a marked



FIGURE 2. World distribution of the pulmonate family Charopidae (Endodontacea); note isolated occurrence on many islands groups, e.g., subantarctic islands, St. Helena Island (Atlantic Ocean), Juan Fernandez Island (W. of South America). Main data supplied by Dr. A. Solem (Chicago).

CHAROPIDAE (= Endodontidae Zilch p.p.)

data after Connolly, 1939 (southern Africa, with corrections)

Burch, 1976 (Australia, interpretation by Dr. A. Solem)

Powell, 1976 (New Zealand, interpretation by Dr. A. Solem)

area	total Pulmonata		Charopidae		Charopidae	
	species	genera	genera	% of total	species	% of total
Southern Africa	635	69	ca. 20	ca. 29%	ca. 120	ca. 19%
Australia	707	188	30	16%	109	15%
New Zealand	294	44	19	43%	145	49%

(some data approximate)

TABLE 3. Local diversity of the pulmonate family Charopidae (Endodontacea) in Africa, Australia and New Zealand.

preponderance of Gondwanaland elements; apart from the Rhytididae and Charopidae most of the other endodontoids and the Bulimulidae and Athoracophoridae (and some other families as well) also belong to this assemblage of taxa.

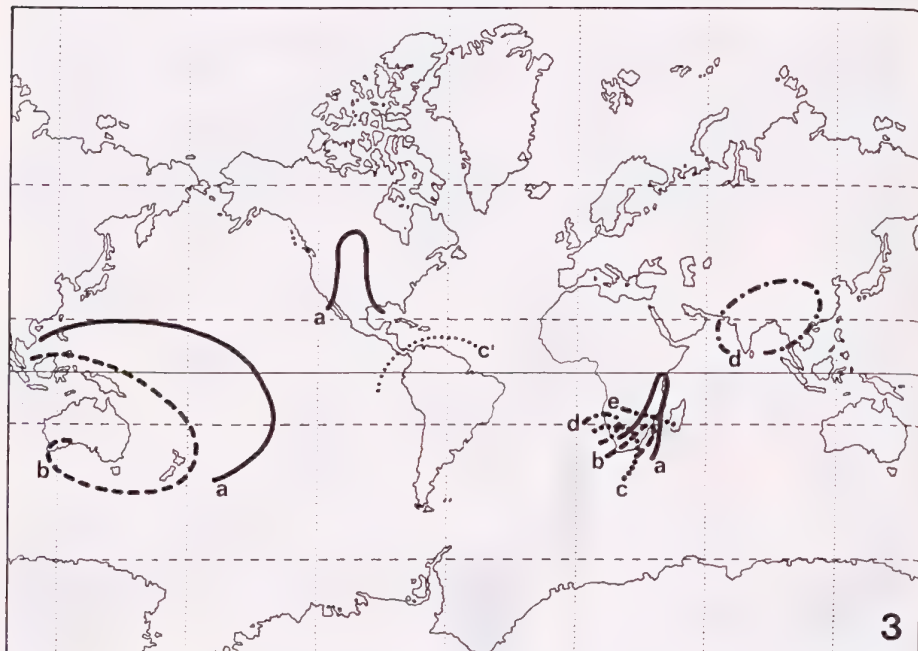


FIGURE 3. Northern limits of Gondwanaland families in Africa and elsewhere; a = Charopidae, b = Rhytididae, c = Dorcasiidae, c' = Strophocheilidae and Megalobulimidae (surmised sister group of Dorcasiidae), d = Corillidae, e = Aperidae.

family	in Africa	in Australasia	elsewhere
Rhytididae	ca. 23° (Transvaal)	ca. 0° (Equator)	ca. 4°30'S (Seychelles)
Aperidae	ca. 19°S (Rhodesia)	—	—
Dorcasiidae	ca. 19°S (South West Africa)	—	sister groups as far north as ca. 11°N (Trinidad and Tobago)
Corillidae	ca. 16°30'S (border of Angola and South West Africa)	ca. 30°N (Tibet)	—
Charopidae	ca. 0° (Equator, Kenya)	ca. 20°N (Marianas and Philippines)	ca. 16°S (St. Helena) ca. 43°N (Idaho, U.S.A.)

TABLE 4. Northernmost limits of the distribution of African pulmonate Gondwanaland families.

Finally attention is drawn to a peculiar phenomenon of the distribution of the Gondwanaland families in Africa: why have these groups in Africa never penetrated as far north as the same families or their (surmised) sister groups have done elsewhere? And why is the diversity of these families so comparatively low in Africa? Table 4 and fig. 3 indicate the northern limits of the various Gondwanaland families discussed here. The map shows that all Gondwanaland families occur well north of the equator outside Africa, while in

Africa only the Charopidae reach the equator. The map also shows the limited area in Africa occupied by the Gondwanaland families. The diversity of these groups has been shown in table 1 and amounts to a total of only five families, ca. 27 genera and ca. 185 species for the whole continent. The evolutionary success of these groups as measured by diversity and area occupied is thus shown to be comparatively very limited.

There may be an explanation for this in the history of Africa through time. Africa has enjoyed an insular existence since losing contact with South America in the Middle Cretaceous, ca. 105 million years B.P., while the connections with Antarctica were already severed in the Upper Jura — both Australia and New Zealand were still connected to Antarctica at the time Africa was already an island. The last link with Antarctica to be cut was that with South America, sometime in the Cretaceous. Africa floated northward and finally collided with the remains of Laurasia, thereby linking up with Europe and Asia. During the Miocene a great and almost continuous forest belt covered large parts of both Asia and Africa, resulting in many forest elements shared by both regions. The following hypothesis may now be considered. After the establishment of the above connection the many and varied land molluscs of Laurasia vigorously started to penetrate Africa, meeting and competing with the Gondwanaland elements already locally present or dispersing northward. By sheer numerical force of the northern elements, as reflected by their present-day diversity, the Gondwanaland families remained restricted in their expansion and distribution. Poor land connections to the north prevented an invasion on a similar scale in the Australian Region, reason why the Gondwanaland families proliferated in that part of the southern hemisphere. The position in America is somewhat different because of the repeated interruption of the connection between North and South America.

Attention should be drawn to the fact that none of the African Gondwanaland families occurs on Madagascar. This island does harbour southern land snail families, but these have distribution patterns that do not include Africa. Madagascar appears to have lost contact with the African continent at a comparatively early stage and has been an island ever since, which may partly account for this phenomenon (see e.g., maps in Cox, 1974).

The above-discussed hypothesis attempting to explain the poor success of the African Gondwanaland snails is seemingly supported by some general data on various groups of invertebrates in Werger's treatise (1978); however, this topic has not been worked out in detail.

An attempt to find support in distribution patterns of plants met with great response from Dr. M.M.J. van Balgooy (Leiden), who supplied maps of four families of Gondwanaland angiosperms: Cunoniaceae, Monimiaceae, Myoporaceae, and Proteaceae. All show tricontinental Gondwanaland distributions and a comparatively low diversity in Africa, and all reach their northern limits outside Africa considerably further north than in Africa. The Proteaceae penetrate far north in Africa, but still reach noticeably higher latitudes in both Asia and Africa. These distribution patterns seemingly confirm the above malacological data and thus may have found their origins in the same causative phenomena.

Climatic factors must have had their own influence. Tropical Tertiary climates may have contributed in driving the temperature Gondwanaland elements southward so that these became concentrated at the southern tips of the southern continents (see e.g., Horton, 1974). This certainly does not seem to apply to the terrestrial molluscs here discussed, unless these subsequently adapted themselves to tropical conditions and moved northward in the areas outside Africa. Rhytididae — Charopidae both occur under fully tropical conditions in e.g. southeast Asia, and the Charopidae are also found in tropical America. This, of course, leaves us with the problem: why did these families become restricted in southern Africa and not elsewhere in the southern continents?

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